Basic Appl. Ecol. **4**, 249–262 (2003)

http://www.urbanfischer.de/journals/baecol

Basic and Applied Ecology

Patterns and processes of biological invasion: The Chinese mitten crab in San Francisco Bay

Deborah A. Rudnick[1]*, Kathryn Hieb[2], Karen F. Grimmer[3], Vincent H. Resh[1]

[1] University of California, Berkeley
[2] California Department of Fish and Game
[3] Monterey Bay National Marine Sanctuary

Received January 23, 2002 · Accepted May 28, 2002

Abstract

The Chinese mitten crab, native to coastal rivers and estuaries of central Asia, has invaded several European countries over the past century, causing widespread concern because of its periodically extreme abundance and burrowing behavior that causes bank erosion. San Francisco Bay and its tributaries contain the first and, currently, only known established population of the Chinese mitten crab in North America. Discovered in South San Francisco Bay in 1992, the mitten crab has spread rapidly to cover several thousand km^2 surrounding the Bay. Between 1995 and 2001, we monitored distribution, population dynamics, and life history attributes of the Chinese mitten crab in San Francisco Bay and its tributaries. Burrow densities increased from a mean of 6 burrows/m^2 in 1995 to >30 burrows/m^2 in 1999 in tidal portions of South Bay tributaries. Mitten crabs are associated with: tidally influenced portions of Bay tributaries as young juveniles; with freshwater streams (≤250 km from their confluence with the Bay) as older, migrating juveniles; and with the open waters of the Bay as reproductive adults after migrating from fresh water to reproduce between late fall and early spring. Population size peaked in 1998, with 750,000 crabs counted in fall migration in a North Bay tributary and 2.5 crabs/tow collected from North Bay breeding grounds; abundance subsequently declined greatly (2500 crabs in the same river system, 0.8 crabs/tow). Average size of adult crabs diverged between the North Bay population, which increased in size between 1996 and 2001, and the South Bay population, which decreased. The rapid establishment and spread of this species, its tolerance for a wide range of biotic and abiotic conditions, and its cyclical population dynamics pose challenges for control.

Die in Flüssen und Ästuaren Zentralasiens beheimatete Chinesische Wollhandkrabbe hat im letzten Jahrhundert einige europäische Länder erobert und verursacht weit verbreitete Bedenken, aufgrund ihrer periodisch auftretenden extremen Häufigkeit und ihres Grabverhaltens, das Ufererosion verursacht. In der Bucht von San Francisco und ihren Zuflüssen befindet sich die erste und bisher einzige etablierte Population der Chinesischen Wollhandkrabbe in Nordamerika. Nach ihrer Entdeckung im Süden der Bucht von San Francisco 1992 hat sich die Wollhandkrabbe schnell über einige tausend Quadratkilometer in der Umgebung der Bucht ausgedehnt. Zwischen 1995 und 2001 untersuchten wir die Verbreitung, die Populationsdynamik und die Eigenschaften der Lebensweise der Chinesischen Wollhandkrabbe in der Bucht von San Francisco und ihren Zuflüssen. Die Dichte der Höhlen nahm in den Gezeitenbereichen der Zuflüsse in der südlichen Bucht von einem Mittelwert von 6 Höhlen/m^2 1995 auf >30 Höhlen/m^2 1999 zu. Wollhandkrabben sind als junge Juvenile mit

***Corresponding author:** Deborah A. Rudnick, Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3112, Phone: +510-642-6315, Fax: +510-642-7428, E-mail: drudnick@nature.berkeley.edu

1439-1791/03/04/03-249 $ 15.00/0

gezeitengeprägten Bereichen der Zuflüsse der Bucht assoziiert, als ältere, wandernde Juvenile mit Süßwasserflüssen (≤250 Kilometer vom Zusammenfluss mit der Bucht) und als reproduktive Adulte mit dem offenen Wasser der Bucht, nachdem sie zwischen Spätherbst und zeitigem Frühjahr zur Reproduktion aus dem Süßwasser eingewandert sind. Die Populationsgröße erreichte 1998 mit 750.000 Krabben ihren Höhepunkt, die während der Herbstmigration in einem Zufluss der nördlichen Bucht gezählt wurden, sowie mit 2,5 Krabben/Schleppzug, die in den **Brutarealen** der nördlichen Bucht gesammelt wurden. Anschließend nahm die Häufigkeit sehr stark ab (2500 Krabben in dem gleichen Fluss, 0,8 Krabben/Schleppzug). Die durchschnittliche Größe der adulten Krabben unterschied sich zwischen der Population der nördlichen Bucht, deren Größe zwischen 1996 und 2001 zunahm, und der Population der südlichen Bucht, bei der sie abnahm. Die rasend schnelle Etablierung und Ausbreitung dieser Art, ihre Toleranz für einen weiten Bereich biotischer und abiotischer Faktoren und ihre zyklische Populationsdynamik stellen eine Herausforderung für ihre Kontrolle dar.

Key words: introduced species – population dynamics – Crustacea – monitoring – life history – burrowing – bay – estuary

Introduction

The Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) was first discovered in San Francisco Bay in the winter of 1992. This non-native crustacean spread rapidly throughout the open waters of the Bay and its tributaries, giving this species the distinction of being one of the most abundant and widely distributed of the more than 200 introduced aquatic organisms found in the Bay (Cohen & Carlton 1998). The recent introduction of this species and its potential for widespread impacts makes *E. sinensis* a timely and important subject for the study of the processes of biological invasion in aquatic ecosystems.

Eriocheir sinensis is catadromous; pelagic larvae are released into coastal waters and metamorphose into benthic juvenile crabs that migrate into brackish and fresh waters. The juvenile crabs spend between 1 and 5 years in freshwater streams and, at sexual maturity, migrate back to saline waters to reproduce. In Asia and Europe, adult, sexually mature crabs (i.e., females with developed secondary structures for carrying eggs; males with mature reproductive organs and/or accessory structures) begin to migrate downstream in late fall and winter. Female *E. sinensis* carry from 250,000 to 1,000,000 eggs attached to the underside of their abdomen. The crabs are believed to have one reproductive season and die shortly after reproduction (Panning 1939).

One of the most often described features of *E. sinensis* is its propensity for burrowing. Juvenile mitten crabs create burrows in banks between the high and low tide lines in tidally influenced portions of streams, and occasionally in muddy banks of freshwater streams. In areas where crabs are particularly abundant, the burrows become tightly packed together and often are interconnected (Rudnick et al. 2000). High burrow densities of the Chinese mitten crab have been linked with bank and levee weakening, and even collapse in some areas into which this species has been introduced (Panning 1939, Dutton & Conroy 1998).

The Chinese mitten crab is native to the rivers and estuaries of central Asia, from the west coast of North Korea to south of Shanghai, China (Panning 1939). The wild population of the crab has severely declined because of a combination of water pollution, dams that block migration to rearing areas, and commercial harvesting (Hymanson et al. 1999). This species has become established, at varying levels of abundance, throughout most of western, central, and northern Europe. In the 1930s, mitten crabs became a serious pest in Germany, causing damage to banks and levees through burrowing activities and to fishing operations through entanglement in nets and injury to netted fish (Panning 1939). The Chinese mitten crab has also been established in France, England, Denmark, Sweden, Finland, Luxembourg, Poland, Austria, Czechoslovakia, and most recently in Portugal and the Seville area of Spain (Hoestlandt 1944, Haahtela 1963, Anonymous 1972, Ingle 1986, Jażdżewski & Konopacka 1993, Dhur & Massard 1995, Clark et al. 1998, Cabral & Costa 1999, Ferrero-Rodriguez pers. comm.). In the Baltic countries, however, the population densities have remained quite low, possibly because the low salinity and/or low temperature of the Baltic Sea inhibits successful reproduction of the Chinese mitten crab (Rassmussen 1987). Likely mechanisms of introduction of the crab to these countries include accidental importation through ballast water or spread to adjacent countries through streams or coastal waterways (Cohen & Carlton 1997).

In North America, a few Chinese mitten crabs have been collected from the Mississippi River (Horwath

1989), Lake Erie (Nepszy & Leach 1973), and the Columbia River Basin (P. Heimowitz pers. comm.). None of these areas, however, currently supports a self-sustaining population of mitten crabs. In California, *E. sinensis* was first collected by commercial shrimp trawlers in the open waters of South San Francisco Bay in 1992, and the population quickly became established and abundant throughout San Francisco Bay and its tributaries. It is likely that mitten crabs arrived in the Bay, as well as in other parts of the continent, either through ballast water or as a result of release of live adult crabs imported for sale in Asian markets (Cohen & Carlton 1997).

The objective of this article is to describe the population dynamics and ecology of the Chinese mitten crab in San Francisco Bay and its tributaries. We describe the invasion history, abundance, distribution, population structure, reproductive patterns, and habitat associations of the Chinese mitten crab throughout this region, and discuss the applications of this research to monitoring and management of this species.

Materials and Methods

Our research efforts focused on three areas of northern California: 1) a regional study of the crab across San Francisco Bay and its tributaries; 2) studies in the tributaries and open waters of South San Francisco Bay; and 3) studies in San Pablo and Suisun Bays, Suisun Marsh, and the Sacramento-San Joaquin Delta (collectively referred to as the North Bay and Delta) (Fig. 1 and Table 1).

Regional data

We collected data on the spread of the mitten crab at a regional level on a continuous basis from 1992 through 1998. Regional distribution data covers all tributaries to San Francisco Bay, including the California Aqueduct and Delta-Mendota Canal that extend to central and southern California. In 1996, the California Department of Fish and Game (CDFG) began to receive numerous reports of collections and sightings of the crabs. These reports, coupled with results of trawls and distribution surveys described below, enabled us to produce maps to describe the distribution of the mitten crab in 1992, 1994, 1996, and 1998.

South San Francisco Bay data

South Bay data were based on: 1) juvenile mitten crabs that were monitored in tidal and freshwater portions of South Bay tributaries; and 2) adult mitten crabs that were collected from the open waters of the South Bay from weekly trawls conducted year-round by the Marine Science Institute (MSI), a nonprofit research and education organization based in the South Bay.

Juvenile mitten crab surveys

In the freshwater tributaries of the South Bay, we conducted research on the population dynamics and habitat associations of juvenile mitten crabs. In 1996, 1999, and 2000, we monitored the distribution of juvenile crabs at 72 sites along 14 tributaries (Fig. 1, South Bay inset). Some of the tributaries are concrete-lined flood control channels that carry water only dur-

Table 1. Origin, methods, dates, and geographic coverage for Chinese mitten crab data

Data collected by	Type of data collected	Methods	Years of data	Geographic coverage
University of California at Berkeley	Juvenile distribution and habitat association	Visual census, trapping	1996, 1999, 2000	South San Francisco Bay tributaries
	Juvenile burrow densities	5 m transects, burrow excavation	1995, 1996, 1999, 2000	Tidally influenced portions of South Bay tributaries
Marine Science Institute	Adult population dynamics and morphology	Otter trawl	1995–2001	Open waters of South San Francisco Bay
California Department of Fish and Game	Juvenile burrow densities	5 m transects	1997, 1998	Suisun Marsh and tidally influenced portions of the Delta
	Adult population dynamics and morphology	Otter trawl	1996–2001	North Bay and Delta
University of California at Davis	Adult population dynamics and morphology	Otter trawl	1996–1999	Suisun Marsh
US Bureau of Reclamation, Tracy Fish Collection Facility	Adult population dynamics and morphology	Collections from fish salvage tanks	1996–2000	southern Delta

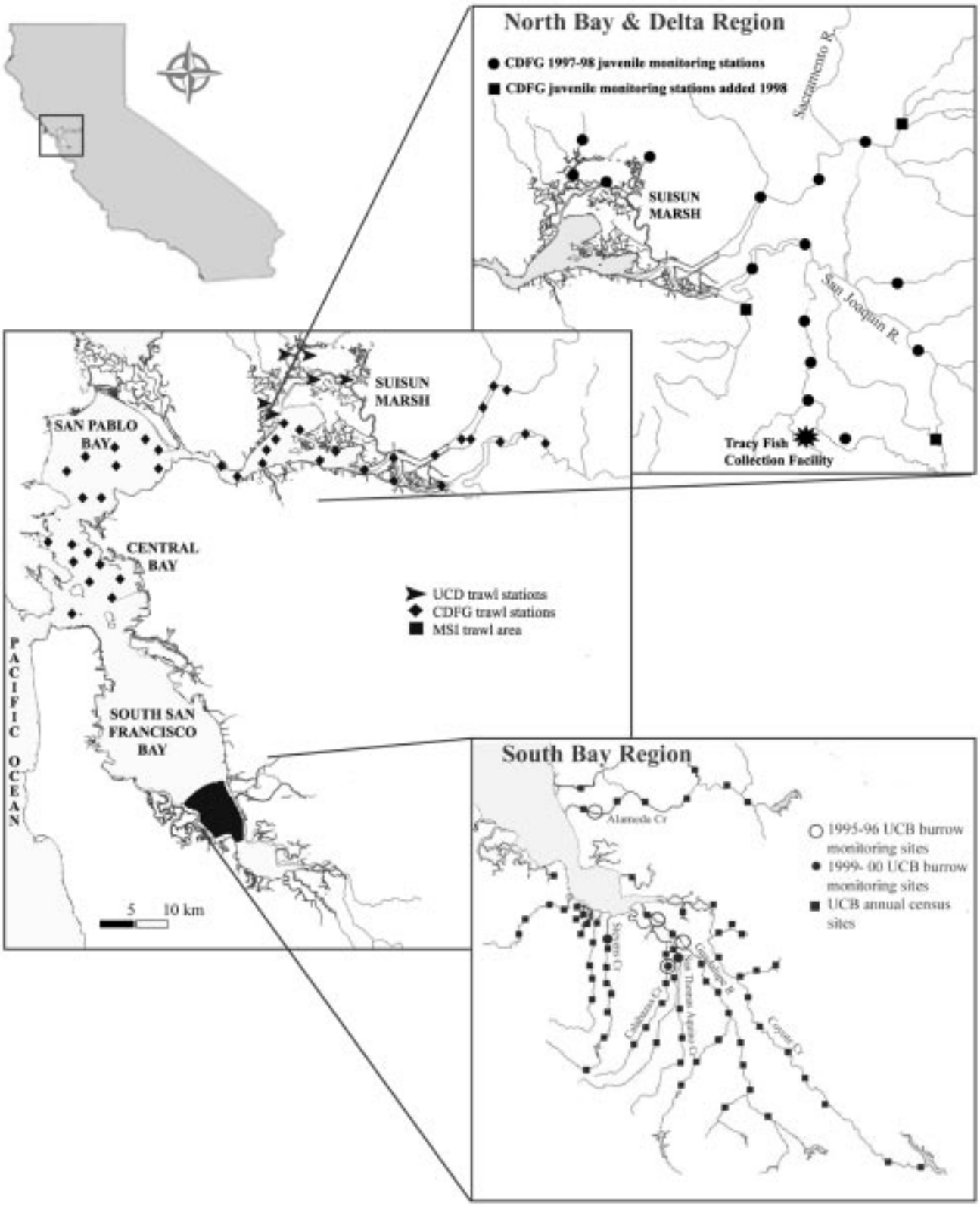

Fig. 1. Regions of study in the San Francisco Estuary. Abbrevations: CDFG = California Department of Fish and Game; UCB = University of California, Berkeley; UCD = University of California, Davis; MSI = Marine Science Institute.

ing storm events; 20 of the 72 sites sampled were this type of concrete channel. A majority of tributaries monitored throughout the South Bay, however, are lined with natural materials, at least along most of their lengths, and confined by set-back levees that allow the river to occupy a restricted portion of its original floodplain. Sites were visited during late summer of each year and were chosen to represent a wide range of salinities, habitat types, and geographical locations throughout the South Bay watershed.

The presence or absence of mitten crabs at each site was established by burrow excavation, setting crab traps, and visually inspecting the area for mitten crabs. Burrows were excavated by hand using trowels. Visual inspection entailed daytime searches for mitten crabs in channel margins, spending at least 30 minutes at a site before concluding that mitten crabs were likely absent.

Habitat parameters associated with the presence or absence of mitten crabs were measured, including: average depth and temperature of water; bank substrate components (clay, silt, organic debris, or gravel); and bank vegetation composition and percent cover. Measurements were not made at sites that were concrete-lined flood control channels because the streams did not provide any natural habitat and were often devoid of water.

In the tidal portions of these freshwater tributaries, we monitored abundance and distribution of mitten crab burrow colonies at four sites during the summer of 1995, 1996, 1999, and 2000 (Fig. 1, South Bay inset). Three sites used in 1995 and 1996 were no longer usable after they received substantial sediment deposition in 1997–98; these sites were substituted in 1999 and 2000 with alternative sites that were similar in salinity and distance from the Bay. The tidally influenced portions of South Bay tributaries range between 0 and 15 ppt in salinity and are up to 8 km in length. The muddy banks of these constrained channels provide ample habitat for juvenile mitten crabs to establish burrows. At each site, burrow density surveys were conducted during the early summer because juvenile mitten crabs are likely to be concentrated in brackish habitats during this time, prior to their upstream migration to freshwater habitats in the late summer and fall (Panning 1939). The same habitat parameters were measured at these sites as were collected for all other surveyed sites (see above).

Burrows were used as a surrogate for estimating local crab abundance because they are easy to measure and provide evidence of crab presence regardless of whether the crab can be seen (Genoni 1991, Mouton & Felder 1996). Chinese mitten crab burrows are easily differentiated from other species' burrows, such as crayfish, because the shape of the crab burrow entrances are elliptical, reflecting the flattened, oval shape of the crab's body. We randomly selected three transects at each site to measure mitten crab abundance; burrow density was calculated as the average of the three transects. Each transect was 5 m in length and ran parallel to the stream channel along the exposed vertical banks; these transects encompassed the distance between the low water line and the high tide mark along the bank. All burrows within each transect were counted to derive the number of burrows/m^2 of bank area. We made estimates of burrow occupancy by conducting burrow excavations of 0.5 m^2 bank area at each site in 1995, 1999, and 2000.

Morphological measurements of crabs collected during surveys were recorded. Size was determined by measuring carapace width (CW) at the widest part of the carapace, just posterior to the fourth antero-lateral spine, and measured to the nearest millimeter with calipers. Sex was determined by the shape of the abdomen for all crabs ≥10 mm CW; in crabs <10 mm, the shape of the abdomen has not yet sufficiently differentiated between males and females to accurately sex the crab.

Adult mitten crab surveys

In the open waters of South San Francisco Bay, the Marine Science Institute (MSI) collected data for adult (i.e. sexually mature) mitten crabs beginning in the fall of 1995; data reported here extend to the spring of 2001. South San Francisco Bay is shallow, with an average depth of 3 m, and bottom sediments are composed mainly of clay and silt. Otter trawls were conducted across 14 contiguous transects, each approximately 0.5 km^2 in area. Data from collected mitten crabs included date of capture, location of trawl capture, number per trawl (catch per unit effort), sex, size (CW), and female reproductive status. At least 100 crabs were measured during each reproductive season. For analysis, we grouped MSI collections for each reproductive season between fall and summer: for example, crabs captured in the reproductive season spanning the fall of 1997 through the summer of 1998 are analyzed as the 1997–1998 group.

North Bay and Delta data

North Bay and Delta *E. sinensis* data were based on: 1) CDFG surveys of juvenile Chinese mitten crabs in Suisun Marsh and the Delta in the summers of 1997 and 1998; 2) CDFG otter trawls conducted monthly at 52 sites (Orsi 1999): mitten crabs have been collected by this survey in the North Bay and Delta since 1996, and data from 1996 to 2001 are reported here; 3) mitten crabs collected from 1996 to 2000 from monthly otter trawls conducted by the University of California at Davis (UCD) in Suisun Marsh (Meng & Moyle

1994, Matern et al. 1996); and 4) collections between 1996 and 2000 of adult Chinese mitten crabs at the US Bureau of Reclamation fish salvage facility, located in the southern Delta (Fig. 1).

Juvenile mitten crab surveys

In the summers of 1997 and 1998, CDFG surveyed juvenile mitten crabs in the North Bay and Delta. In 1996, four sites in Suisun Marsh and 11 in the Delta were sampled; in the summer of 1998, four Suisun Marsh sites and 14 sites (three new sites not sampled in 1997) in the Delta were sampled (Fig. 1, North Bay and Delta inset). Sampling was done at a minus low tide, when a maximum area of bank was exposed. At each site, all burrows, ponded water, vegetation, and debris were searched for mitten crabs along a 5 m transect parallel to the stream channel; the height of these transects encompassed the distance between the low water line and the high tide mark along the bank. Two transects were conducted at each site (except for two sites where exposed bank was only sufficient for one transect), with the second transect being within 0.5 km of the first transect.

Crabs were measured and sexed using the same protocols as in the South Bay juvenile study. Additional information recorded included vegetation and soil types, bank profile, salinity (ppt), and water temperature (°C). Crab density is total number of crabs collected at each site divided by the total area sampled (m^2) at each site for the year.

Adult mitten crab surveys: North Bay and Delta

Up to 30 *E. sinensis* from each CDFG station were randomly selected, measured (CW), and sexed (ovigerous females were noted); the remainder of mitten crabs collected in each trawl was counted. Physical data collected at each station included a water column profile of temperature (°C) and salinity (ppt).

Because a brackish water gradient extending from San Pablo and Suisun bays into the lower San Joaquin and Sacramento Rivers results in a large overlap of juvenile and adult crab habitat, multiple year-classes of Chinese mitten crabs probably co-occur throughout this region. For the North Bay and Delta population, therefore, we used size-frequency histograms to distinguish adult from juvenile mitten crabs. Based on examination of the size frequency data we defined adult mitten crabs as females > 32 mm CW and males > 39 mm CW.

An annual North Bay and Delta *E. sinensis* catch per unit effort (CPUE) was calculated as the average number of crabs per tow from October through March of the following year. Samples were not collected upstream of San Pablo Bay in January 1997, and were not collected throughout the region in November and December 1999 and March 2001; CPUE was not adjusted for these missing data. Given the large numbers of crabs collected in other years during these months, the calculated CPUE for 1996–97, 1999–2000 and 2000–01 likely are underestimates.

Adult mitten crab surveys: Suisun Marsh

Crabs from UCD trawls were sexed and measured as described for the CDFG and South Bay surveys. Physical data collected at each station included temperature (°C) and salinity (ppt). Crabs were first collected in February 1996, but adult crabs migrating downstream were not collected until fall 1997. For this reason, only data from 1997 on were used for analyses.

Adult mitten crab surveys: southern Delta

The US Bureau of Reclamation Tracy Fish Collection Facility (TFCF) collects Chinese mitten crabs that enter the facility during their downstream migration. The TFCF is located just upstream of power turbines and is designed to collect fish and transfer them safely away from the turbines. The Bureau collected size and sex data on these crabs beginning in 1997; at least 500 crabs were measured during each migration season. In addition, time of collection was recorded by the facility in order to describe diel timing of migration patterns. The TFCF tracked the mitten crab population entering the facilities using 10-minute counts every two hours. Combined with counts of crabs collected at water intake points and specially installed traps in 1998 and 1999, daily estimates of the total number of crabs collected at these facilities were made.

Results

Distribution and abundance

Regional distribution

The distribution of the Chinese mitten crab expanded dramatically over the course of this study. Crabs were restricted to the South Bay in 1992, were found throughout the open waters and immediate tributaries to the main body of the Bay in 1994, were distributed throughout the central and western Delta and South Bay tributaries by 1996, and had expanded their distribution to the Sacramento and San Joaquin Rivers and their tributaries by 1998 (Fig. 2).

Juvenile distribution and abundance

Between 1996 and 2000, juvenile crabs rapidly spread within the South Bay and its tributaries. In 1996, we observed mitten crabs several km upstream in South Bay tributaries; by 1999 and 2000, they occurred up to 50 km upstream from the Bay (Fig. 3).

Burrow densities of juvenile crabs in South Bay tributaries increased dramatically between 1996 and 1999 (Fig. 4). At the four South Bay sites examined for juvenile abundance in 1995, burrow densities ranged from 3 to 12 burrows/m^2 (all sites: 6.3 ± 1.2, mean ± s.e.); densities were similar in 1996. In 1999, burrow densities ranged from 21/m^2 to 39/m^2 (all sites: 30.0 ± 1.6, mean ± s.e.). In 2000, the mean density of all surveyed sites (21.1 ± 2.1, mean ± s.e) declined significantly ($p < 0.05$, t test).

Based on excavations, average occupancy rates of mitten crab burrows in South Bay sloughs decreased over time, from 80% in 1995, to 64% in 1999, and to 58% in 2000. The combined occupancy rates and burrow densities yielded estimated population densities of 5 crabs/m^2 in 1995, 19/m^2 in 1999, and 12/m^2 in 2000 (Fig. 4).

In the North Bay and Delta, densities of juvenile mitten crabs remained low throughout the sampling period (Fig. 5). Suisun Marsh densities in 1997 and 1998 ranged between 0.4 and 1.7 crabs/m^2 in 1997, and 0.3 and 3.0 crabs/m^2 in 1998 (Fig. 5). In the Delta, densities ranged between 0 and 0.4 crabs/m^2 in 1997, and 0 and 1.0 crabs/m^2 in 1998.

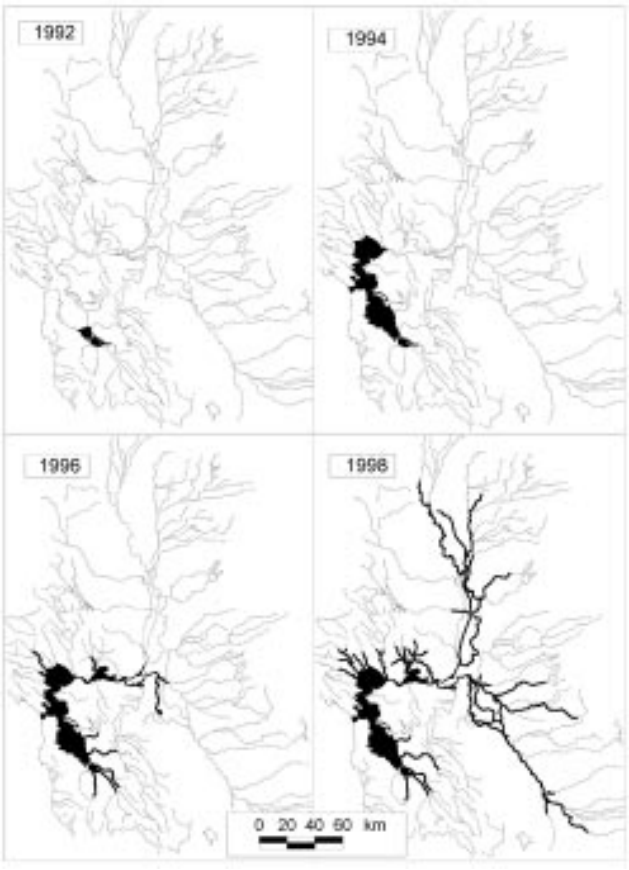

Fig. 2. Changes in regional distribution, indicated in bold black, of the Chinese mitten crab in the San Francisco Bay catchment, 1992–1998.

Adult distribution and abundance

Between 1995 and spring of 1999, abundance of adult mitten crabs in South San Francisco Bay was relatively constant. The highest catch per unit effort (CPUE), nearly double that of any previous year, was in the 1999–2000 reproductive season (Fig. 6). Adult crabs were first collected in the North Bay and Delta by CDFG trawls in fall 1996; abundance of crabs there increased dramatically in the 1998–99 reproductive season, and then declined in 1999–2000 (Fig. 6).

Collections of adult, downstream-migrating crabs at the TFCF in the southern Delta reflected the same trends in abundance as seen in North Bay and Delta trawl data.

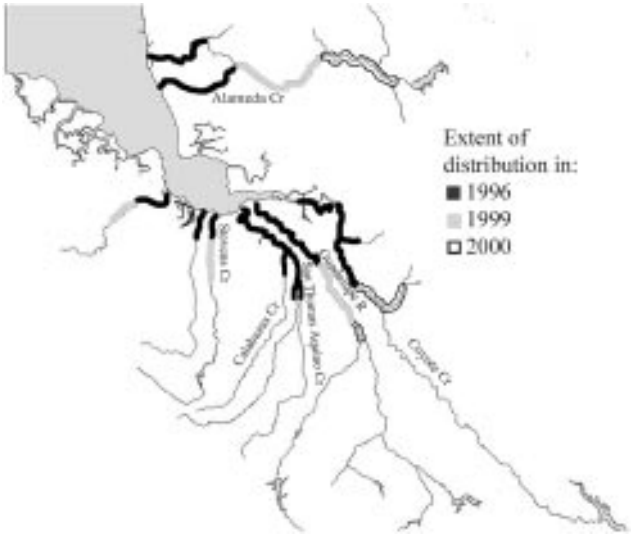

Fig. 3. Changes of distribution of juvenile crabs in the South San Francisco Bay catchment, 1996–2000; see Fig. 1 for the location of this map.

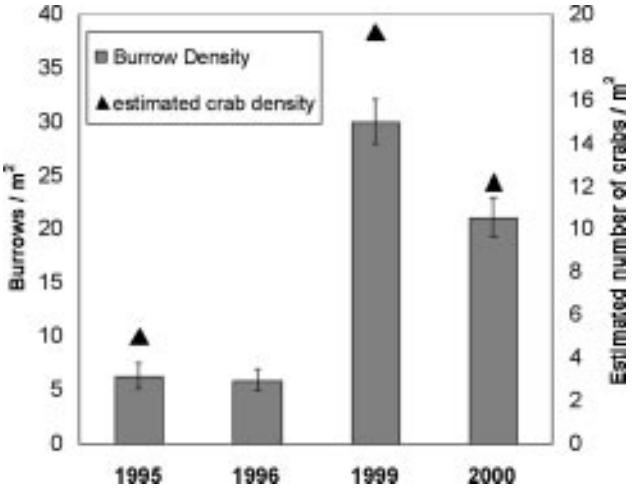

Fig. 4. Average burrow densities of juvenile crabs in South Bay tributaries: error bars are ± 1 s.e; 4 sites were sampled each year. Crab density estimates were generated by multiplying burrow occupancy rates by burrow densities. No occupancy rate data were collected in 1996.

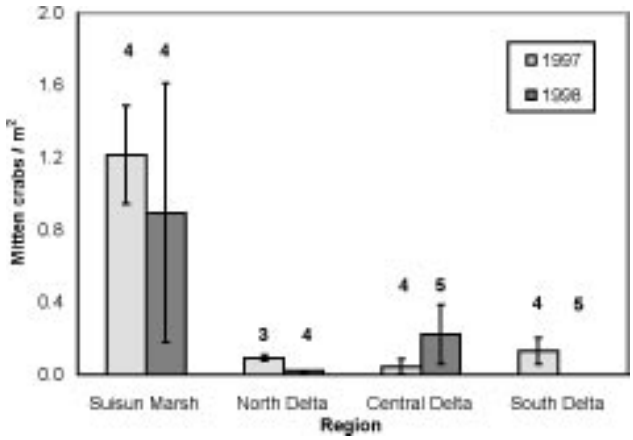

Fig. 5. Densities per m^2 of juvenile crabs in Suisun Marsh and in three regions of the Delta. Error bars are ± 1 s.e; numbers above the bars are number of sites sampled in each region in each year.

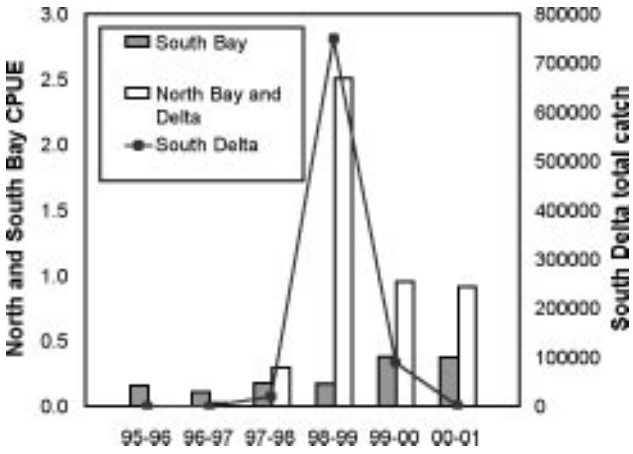

Fig. 6. Number of adult crabs caught in three areas of the San Francisco Bay catchment; data is grouped from fall of one year to summer of the following year to incorporate the entire reproductive season into a sampling period.

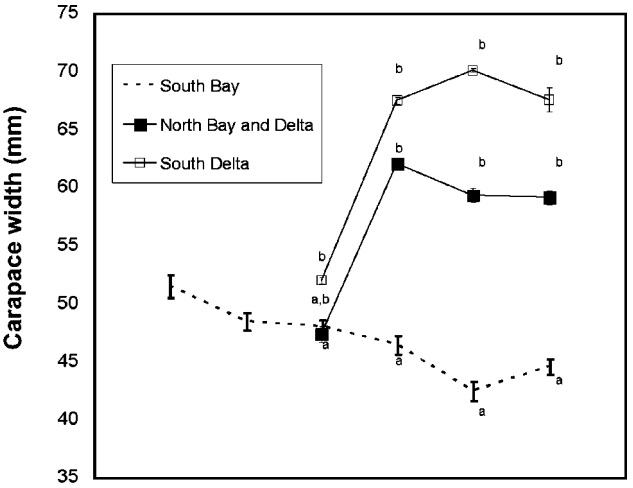

Fig. 7. Average size (mean ± 1 s.e.) of Chinese mitten crab adults during the reproductive season in three areas of the San Francisco Bay catchment, 1995–2001: North Bay and Delta and South Delta crabs (b) are significantly larger than South Bay crabs (a) in years 1998–2001 (Tukey HSD, $p < 0.001$).

Fewer than 100 crabs were collected at the facility in the fall of 1996. However, approximately 20,000 crabs were collected at TFCF during the fall of 1997, and an estimated 750,000 crabs were collected at TFCF in the fall of 1998. In 1999, collections at the facility declined dramatically and remained low in 2000 (Fig.6).

Population structure

At the four tidally influenced, burrow-monitoring sites in the South Bay, juvenile mitten crabs ranged in size from 5 to 35 mm CW (mean ± s.e. = 18 ± 0.6 mm, n = 230). Crabs > 35 mm CW and up to 80 mm CW were found at freshwater survey sites.

Adult, sexually mature crabs collected in the open waters of the South Bay ranged in size from 30 mm CW to 80 mm CW; adults collected from North Bay trawls ranged in size from 33 mm to 84 mm CW; downstream-migrating adults collected at the TFCF ranged in size from 40 mm to 95 mm CW. Size did not differ significantly by sex for this population, nor did size vary significantly within the reproductive season for either sex.

Over the first five years of collections from South San Francisco Bay, there was a continual decline in the yearly average size of adult crabs; in contrast, the mean size of all adult crabs collected in the North Bay and southern Delta increased from 1997 to1999 and showed little change in 2000–01 (Fig. 7). North Bay and southern Delta collections were significantly larger than the average sizes of crabs collected in the South Bay between 1998 and 2001 (ANOVA, Tukey HSD $p < 0.001$) (Fig. 7).

The sex ratio of adult mitten crabs collected from both the South Bay and North Bay and Delta exhibited a consistent pattern of a greater proportion of males in the fall and early winter giving way to a higher proportion of females in the spring (Fig. 8). During nearly all years of the study period, the sex ratio of collected crabs was slightly biased towards males: in the South Bay, 55% of collected crabs were male; in North Bay and Delta trawls, 58% of all adults collected were males; and adult males collected from Suisun Marsh slightly outnumbered females (52%).

Reproductive patterns

In the southern Delta, adult mitten crabs migrating downstream to their reproductive grounds were collected nearly exclusively in the fall months. Mitten crabs arrived in low numbers at TFCF in late August or early September during all years of monitoring, with daily catches peaking between mid-September and early October (Fig. 9). Downstream crab migration through TFCF showed a strong diel pattern. Mitten crabs entered the holding tanks at the highest rates

during the late evening and early morning hours; entries declined during the day (Fig. 10).

Adult mitten crabs in the North Bay and Delta moved from shallower, fresher waters in the fall to deeper, more saline waters in winter and early spring. During the late summer through the early reproductive season (October-November), adults were most common in the lower rivers and in the shallow waters of Suisun Bay. Over December and January, there was a continued migration downstream to San Pablo Bay (Fig. 11). Adult mitten crabs were most commonly collected during the winter months in the deepest waters of San Pablo Bay.

Adult males and non-ovigerous females continued to be collected upstream of San Pablo Bay after January. Most ovigerous females, however, were collected in San Pablo Bay; only 9% were collected upstream of San Pablo Bay and none were collected upstream of Suisun Marsh. From April–August, a few non-ovigerous females were collected in San Pablo Bay. We assume that these females were post-reproduction because many appeared to be sluggish, missing appendages and covered in epizooids, indicating that they had been in salt water for several months.

Ovigerous females were collected from October to June, with the highest percentage of ovigerous females collected in the late fall and early winter of each reproductive season (Fig. 8). Over one-half of all females collected between November and April from both the North Bay and Delta and the South Bay were ovigerous.

Habitat associations

We found mitten crabs throughout three different habitats in San Francisco Bay and its tributaries: tidal channels (tributaries influenced by tidal inflow); freshwater creeks (tributaries upstream of tidal influence); and the open waters of the South, Central, San Pablo, and Suisun Bays. Salinity differed among the three habitats, ranging from 1–15 ppt in tidal sloughs, <1 ppt in freshwater creeks, and 15–35 ppt in the Bays.

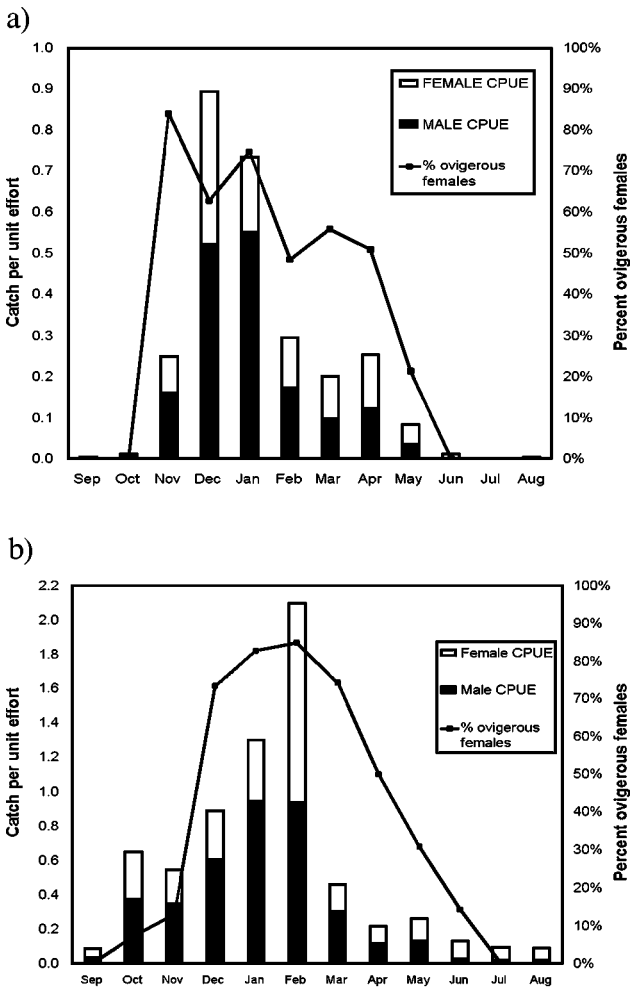

Fig. 8. Sex ratios and rates of ovigerity of adults crabs from a) South Bay trawls and b) North Bay and Delta trawls within the reproductive season. Months are averaged over the years of the data set.

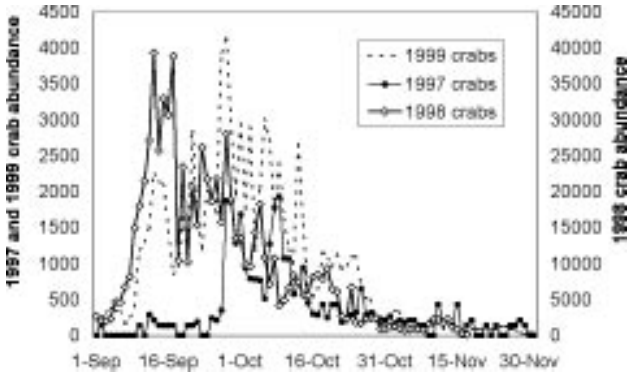

Fig. 9. Daily counts of crabs caught at the Tracy Fish Collection Facility in fall 1997, 1998, and 1999.

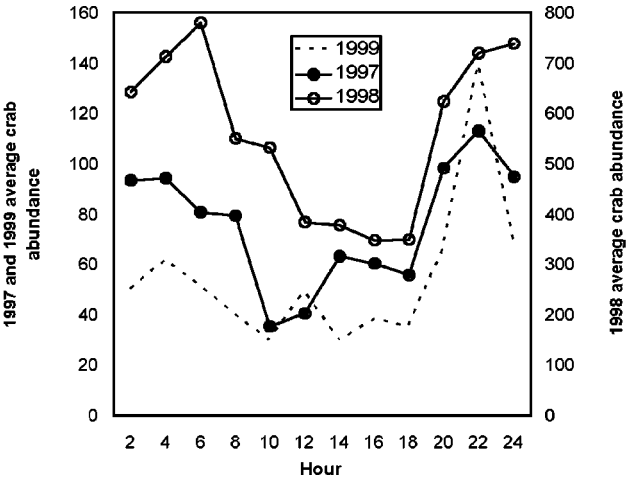

Fig. 10. Diel distribution of migrating crabs caught at the Tracy Fish Collection Facility: number of crabs per two-hour intervals were extrapolated from 10-minute counts; data from two-hour intervals were averaged for all collections made between September 1 and November 30 of each year.

Juvenile habitat associations

Juvenile crabs were uncommon in the open waters of the Bay. Of 915 crabs collected and measured from the open waters of the South Bay, 14 (2%) were smaller than the smallest reproductive female and considered as juveniles (<30 mm CW). Of the 1338 crabs collected by trawl in the open waters of the North Bay and Delta, 142 (11%), were juveniles.

Burrows of juvenile crabs were mainly found in tidally influenced sloughs within a few km of the open

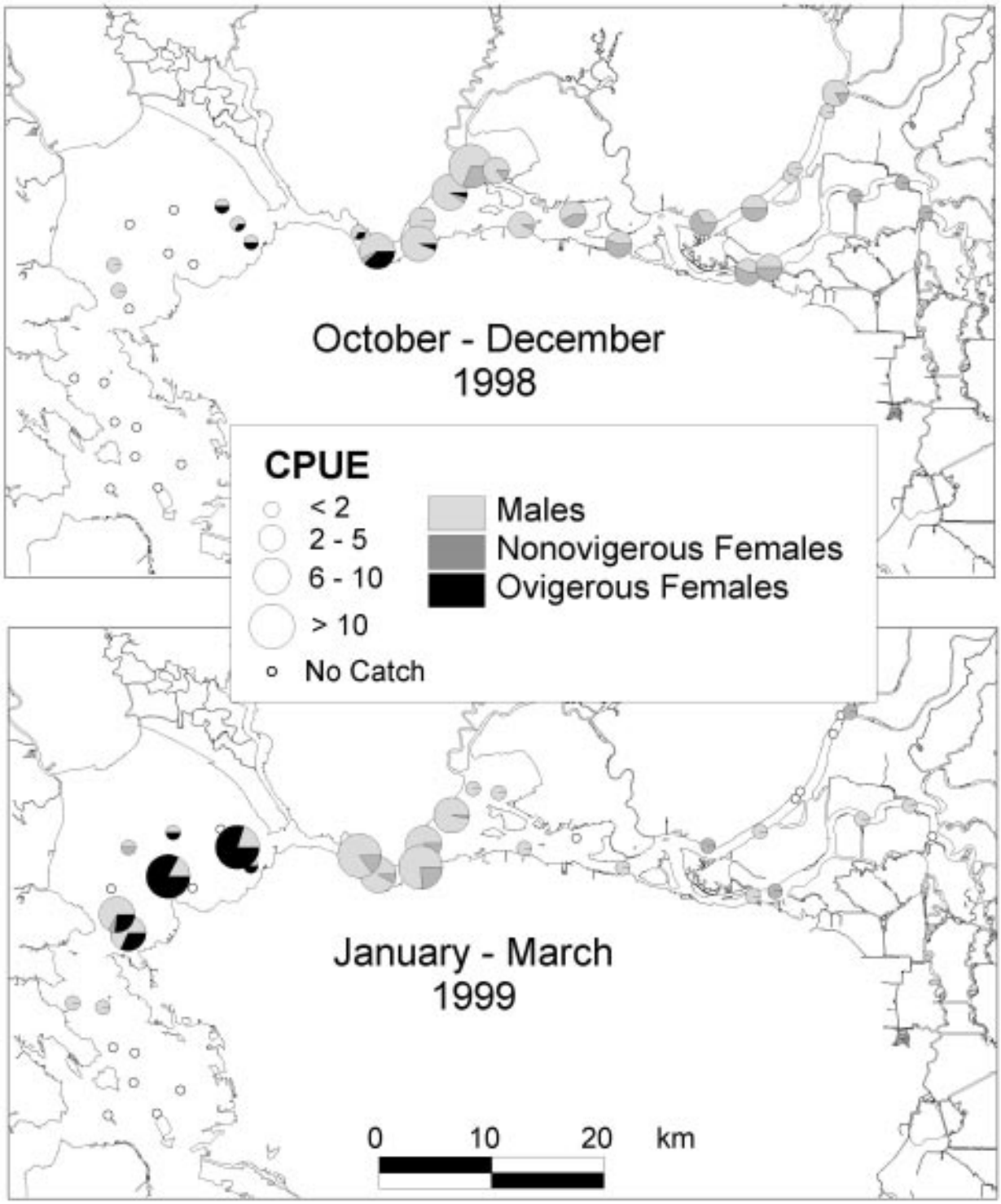

Fig. 11. Distribution of adult crabs in the North Bay and Delta during the 1998 –1999 reproductive season.

waters of the South Bay. Burrows were associated with banks with a high clay and silt content. Bank slopes where burrowing was found included a few nearly flat (5°) banks but a majority were in steep banks (≥35°). Vegetative cover was highly variable, ranging from banks essentially bare of cover to complete cover, usually by *Typha* or *Scirpus spp*. Stream temperature in channel thalwegs ranged from an average of 14.0 °C ± 1.0° (mean ± s.e.) in the winter to 20.0 °C ± 0.8° in summer (n = 8 streams). Although nearly all burrows were exposed above water during some part of the tidal cycle, we found (upon excavation) that the downward slope inside the burrows, combined with the moisture in the bank, retained water at the back end of the burrow.

Surveys of juvenile mitten crabs in South Bay tributaries upstream of tidal influence revealed a wide range of habitat associations. Mitten crabs were found in freshwater creeks openly foraging on the substrate, associated with macrophytes on stream margins, and underneath roots, rocks, and debris in the stream channel. Occasionally, small burrow colonies were found at stream margins where the substrate appeared soft enough for burrowing; generally, however, burrows were not found in freshwater portions of streams. Crabs were rarely found in concrete-lined portions of channels.

The highest densities of juvenile mitten crabs in the North Bay and Delta were associated with shallow, vegetated areas with natural or reinforced cobble banks. Vegetation at these sites consisted mainly of *Scirpus* and *Egeria densa*. In both years of the CDFG juvenile monitoring study, salinity at low tide was highest in Suisun Marsh (1997 mean = 5.4 ppt, 1998 mean = 0.9 ppt) and lowest in the northern Delta (1997 mean = 0.07 ppt, 1998 mean = 0.06 ppt), with low salinities in both the central and southern Delta. In 1997, there appeared to be a strong positive correlation between salinity and juvenile densities at different sites (r = 0.77); this correlation, however, was weak though still positive, in 1998 (r = 0.16).

Adult habitat associations

E. sinensis were collected in the North Bay and Delta from a wide range of salinities (fresh water to 30 ppt) and temperatures (7 to 21 °C) during the reproductive season. Ovigerous females were, on average, collected at the highest salinity (mean = 18.1 ppt). Adult males and non-ovigerous females were collected at similar salinities (mean = 11.6 ppt for males; 10.9 ppt for females).

Gear and sampling methods limited South Bay trawls to an area relatively homogeneous in salinity and depth; thus, we were unable to discern any differences in adult habitat distribution in this area.

Discussion

Distribution and abundance

The Chinese mitten crab has rapidly spread throughout San Francisco Bay and its tributaries since its initial discovery in 1992. As of 2000, the range of the Chinese mitten crab included several hundred km^2 of freshwater and estuarine habitats, making the crab one of the most widely spread aquatic invasive species in the western United States. It is probable that the crab's distribution exceeds our estimates, as low densities in upper reaches of tributaries made crabs harder to find. Chinese mitten crabs can undertake enormous migrations and have been found as far as 1000 km upstream in China (Gollasch 1999). The Chinese mitten crab is known only to be limited in its upstream migration by major impediments such as large dams; mitten crabs have been known to leave the water to circumnavigate such obstacles (Panning 1939; Dan 1984). We expect that within the next few years, all river systems with connections to and within several hundred km from San Francisco Bay, and downstream of any major dams or man-made structures, will contain these crabs.

Because the North Bay and Delta differs dramatically from the South Bay in terms of salinity gradient and habitat types, and because survey methods differed for these two regions, it is difficult to directly compare the densities of juvenile mitten crab populations. The closest comparison might be drawn between surveys conducted in Suisun Marsh and South Bay tributary surveys, because both regions have similar salinities and earthen channels with banks dominated by silt and clay. Densities of juvenile mitten crabs in Suisun Marsh are far lower than those found in South Bay tributaries. This difference may arise from: 1) more habitat being available to juvenile mitten crabs among the numerous small channels feeding Suisun Marsh, leading to juveniles spreading out in the Marsh; and 2) the greater abundance of aquatic vegetation in shallow, open waters that may provide an alternative habitat to building burrows. More frequent collections of juveniles from trawls in open waters in the North Bay and Delta than in the South Bay support this theory of alternative habitat use.

Both the increase in burrow densities in the South Bay and the increase in CPUE of trawled adults in the South Bay, North Bay, and Delta during the period of this study indicate that the population growth rate increased between 1996 and summer of 1999. The decline in South Bay burrow densities in the summer of 2000, and in North Bay CPUE and TFCF collections in 1999–2000, suggests a population decrease. Because South Bay trawls are conducted on fixed tran-

sects, it cannot be determined whether the increase in CPUE in 2000 resulted from a population increase or another cause, such as a shift in the breeding grounds of the crabs within the South Bay.

Fluctuations in abundance over the six years of the study suggest an oscillatory population dynamic that has been reported in several other countries in which the crab has become established (Hoestlandt 1944, Clark et. al 1998, Gollasch 1999); however, we do not yet have the long-term data required to confirm such a pattern. European populations have rebounded after each decline, indicating that a multiple-year decrease in population size may not mean that the species is disappearing from the system.

Population structure

The spatial size distribution that we have documented for juvenile mitten crabs matches the pattern we would expect given the crab's migratory patterns. It is not currently known how well size correlates with age but, assuming that larger crabs are older than the smaller ones, average age of the crabs increases with increasing distance from the mouths of South Bay tributaries. This pattern is consistent with reports from China and Europe that mitten crabs migrate upstream to new areas during development (Panning 1939, Veldhuizen 2000). Based on the wide ranges of crabs that we found in brackish and freshwater habitats throughout the year, it is probable that there are at least two year-classes of crabs inhabiting the streams during most of the year.

The size divergence observed between South Bay and North Bay and Delta adult Chinese mitten crabs supports anecdotal observations by researchers over the past several years that there is a size difference that separates the two populations (Zhao 1999, Veldhuizen 2000). The reasons for this differentiation are unclear, although the pattern of invasion, which suggests a single source population spreading from South San Francisco Bay, suggests that the divergence is a result of environmental differentiation among the habitats used by these populations rather than a result of genetic differentiation.

Reproductive patterns

The temporal pattern of downstream migration to and arrival in the brackish open waters of San Francisco Bay in fall and early winter agrees with the pattern that has been described for this species throughout the world (e.g., Panning 1939, Hymanson et al. 1999). Both South and North Bay data suggests that male mitten crabs begin migrating down to the Bay earlier in the reproductive season, which is similar to patterns observed in European populations (Hoestlandt 1944). There is a strong diel component to the pattern of migration, with adults migrating downstream more actively at night than during the day; this behavior may benefit the crab by reducing visibility and therefore risk of predation. Females appear to remain in the open waters of the Bay longer than do males.

The pattern whereby ovigerous females are collected from open waters of the Bay between October and June, with the greatest rates of ovigerity for these populations occurring in early winter, fits with our observations that newly metamorphosed juveniles are observed in South Bay sloughs from early spring through early summer. This timing agrees with literature that reports a one- to three-month larval period, followed by settling and migration into freshwater tributaries (Anger 1991, Kim & Hwang 1995).

The salinities at which we collected ovigerous females were generally far lower than the salinities associated with ovigerous Chinese mitten crabs in other studies. Some literature suggests that female Chinese mitten crabs require marine salinities (>30 ppt) in order for eggs to adhere to the pleopods (Panning 1939, Ingle 1986; but see Hymanson et al. 1999); however, ovigerous females we collected were found in brackish waters of approximately 18 ppt. Previous assumptions about the life history of the crab may need to be reexamined in light of this finding.

While crabs in China show a pattern of smaller crabs arriving to breeding grounds early in the reproductive season, followed later by larger individuals (Zhao 1999), our data does not show any discernable pattern of sizes within the reproductive season.

Habitat associations

Newly metamorphosed juveniles move from the body of the Bay to the tidally influenced areas of its tributaries, and were found to be most common in areas of: 1) low salinity (< 6 ppt); and 2) steep, clay banks lined with *Scirpus* spp. and *Typha latifolia* in the South Bay; and 3) shallow waters with abundant submerged macrophytes in the North Bay and Delta.

Eriocheir sinensis tolerates a wide range of abiotic factors. All three regions of the world in which *E. sinensis* occur exhibit a temperate climate; however, the temperature range mitten crabs encounter within these regions is large, and laboratory studies underscore the crab's ability to tolerate a wide range of temperatures (Anger 1991). The Chinese mitten crab has exhibited a remarkable ability to survive in highly modified aquatic habitats, as it encounters highly altered and polluted waters in many parts of its native and introduced ranges (Hoestlandt 1944; Ingle 1986; Hymanson et al. 1999). Certainly its success in San Francisco Bay and

its tributaries is evidence of its ability to survive in aquatic systems that have been highly modified and impacted by humans (Nichols et al. 1986).

In conclusion, this study of the Chinese mitten crab is the most comprehensive documentation of the spread of an invasive species in the San Francisco Bay and its tributaries. However, it is crucial that monitoring continue to gather long-term data on the crab's population dynamics and impacts. Control of this species will be difficult because of its abundance, ubiquity, high reproductive rate, and wide range of physiological tolerances. The differences displayed between North and South Bay crabs suggest that the species cannot be managed as a single population. Ongoing research will strengthen our understanding and guide management of this established population, as well as provide information to those concerned with prevention and early detection of this species in regions that do not yet have the Chinese mitten crab.

Acknowledgements. The authors thank the Marine Science Institute, Redwood City, CA, for providing staff time and equipment, the USBR Tracy Fish Collection Facility for sharing data, Lydia Cao, Leah Rogers, and Catherine Ryan (UC Berkeley) for field assistance, Tanya Veldhuizen (California Department of Water Resources) for survey work and for providing data and commentary, Anna Holmes and Jenn Olan (CDFG) for field assistance, Scott Matern and Robert Schroeter (UC Davis) for the Suisun Marsh trawl data, funded by the California Department of Water Resources, and the Santa Clara Valley Water District for access to study sites. Intellectual support was provided by many of our colleagues on the Interagency Ecological Project's Chinese Mitten Crab Project Work Team. This research has been supported by grants from CALFED, the University of California Water Resources Center as part of Water Resources Center Project UCAL-WRC-W-881, and by the Interagency Ecological Program for the San Francisco Estuary.

References

Anger K (1991) Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsidae). Marine Ecology Progress Series 72: 103–110.

Anonymous (1972) Report of the working group on introduction of non-indigenous marine organisms. International Council for the Exploration of the Sea, Charlottenlund, Denmark.

Cabral H, Costa M (1999) On the occurrence of the Chinese mitten crab, *Eriocheir sinensis* in Portugal (Decapoda, Brachyura). Crustaceana 72: 55–58.

Clark P, Rainbow P, Robbins R, Smith B, Yeomans W, Thomas M, Dobson G (1998) The alien Chinese mitten crab, *Eriocheir sinensis* (Crustacea: Decapoda: Brachyura), in the Thames catchment. Journal of the Marine Biological Association, U.K. 78: 1215–1221.

Cohen A, Carlton J (1997) Transoceanic transport mechanisms: introduction of the Chinese mitten crab, *Eriocheir sinensis*, to California. Pacific Science 51: 1–11.

Cohen A, Carlton J (1998) Accelerating invasion rate in a highly invaded estuary. Science 279: 555–558.

Dan Q (1984) The ecological study on the anadromous crab *Eriocheir sinensis* going upstream. Tung wu hsueh chih (Chinese Journal of Zoology) 6: 19–22.

Dhur G, Massard J (1995) Étude historique et faunistique des invertébrés immigrés ou introduits dans la Moselle luxembourgeoise et ses affluents. Bulletin de la Societé Naturelle Luxembourg 96: 127–156.

Dutton C, Conroy C (1998) Effects of burrowing Chinese mitten crabs (*Eriocheir sinensis*) on the Thames tideway. Environment Agency report, London, U.K. April.

Genoni G (1991) Increased burrowing by fiddler crabs *Uca rapax* (Smith) (Decapoda: Ocypodidae) in response to low food supply. Journal of Experimental Marine Biology and Ecology 147: 267–285.

Gollasch S (1999) Current status on the increasing abundance of the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1854 in German rivers. Proceedings of the first annual meeting on the Chinese mitten crab in California, Sacramento, CA. 23 March.

Haahtela I (1963) Some new observations and remarks on the occurrence of the mitten crab, *Eriocheir sinensis* Milne-Edwards (Crustacea, Decapoda), in Finland. Aquilo, Series Zoologica 1: 9–16.

Hoestlandt H (1944) Le crabe Chinois (*Eriocheir sinensis* Mil. Ed) en Europe et principalement en France. Annales des Épiphyties 3: 223–233.

Horwath J (1989) Importation or shipment of injurious wildlife: mitten crabs. Federal Register 54(98): 22286–22289.

Hymanson Z, Wang J, Sasaki T (1999) Lessons from the home of the Chinese mitten crab. Interagency Ecological Program Newsletter 12(3): 25–32.

Ingle R (1986) The Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards – a contentious immigrant. The London Naturalist 65: 101–105.

Jażdżewski K, Konopacka A (1993) Survey and distribution of Crustacea Malacostraca in Poland. Crustaceana 65: 176–191.

Kim C, Hwang S (1995) The complete larval development of the mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Decapoda, Brachyura, Grapsidae) reared in the laboratory and a key to the known zoeae of the Varuninae. Crustaceana 68: 793–812.

Matern S, Meng L, Moyle P (1996) Trends in fish populations of Suisun Marsh, January–December 1995. Report no. B-59998. Department of Water Resources, Stockton, CA.

Meng L, Moyle P (1994) Changes in abundance and distribution of native and introduced fishes in Suisun Marsh. Transactions of the American Fisheries Society 123: 498–507.

Mouton E, Felder D (1996) Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and

Uca longisignalis in a Gulf of Mexico salt marsh. Estuaries 19: 51–61.

Nepszy S, Leach J (1973) First records of the Chinese mitten crab, *Eriocheir sinensis*, (Crustacea: Brachyura) from North America. Journal of the Fisheries Research Board of Canada 30: 1909–1910.

Nichols F, Cloern J, Luoma S, Peterson D (1986) The modification of an estuary. Science 231: 567–573.

Orsi J (1999) Report on the 1980–1995 fish, shrimp and crab sampling in the San Francisco Estuary, California. Interagency Ecological Program, Stockton, CA.

Panning A (1939) The Chinese mitten crab. Smithsonian Institution annual report for 1938, Washington, D.C.

Rassmussen E (1987) Status over uldhåndskrabbens (*Eriocheir sinensis*) udbredelse og forekomst i Danmark. Flora og Fauna 93: 51–58.

Rudnick D, Halat K, Resh V (2000) Distribution, ecology and potential impacts of the Chinese mitten crab (*Eriocheir sinensis*) in San Francisco Bay. University of California Water Resources Center contribution no. 206, Riverside, CA.

Veldhuizen T (2000) Predictions and predications from a visiting Chinese mitten crab expert. Interagency Ecological Project Newsletter 13(1): 14–15.

Zhao A (1999) Ecology and aquaculture of the Chinese mitten crab in its native habitat. Meeting of the Interagency Ecological Project Chinese mitten crab project work team, Richmond, CA. 26 August.